# CLUTCH SIZE AND OFFSPRING SIZE IN THE WOLF SPIDER *PIRATA SEDENTARIUS* (ARANEAE, LYCOSIDAE)

**Christopher A. Brown,**[1] **Bridget M. Sanford** and **Rebekah R. Swerdon**: Dept. of Biology, State University of New York College at Fredonia, Fredonia, New York 14063 USA

**ABSTRACT.** Wolf spiders in the genus *Pirata* are common, often locally abundant, inhabitants of many moist or mesic habitats. However, relatively little is known about the ecology or life history of these spiders. Here we present data collected during 2000–2001 on female size, offspring size and clutch size for two populations (Ball Gulf, Hardscrabble Creek) of *Pirata sedentarius* from western New York. In both populations, mean offspring size was less variable than was female size, clutch size or total clutch mass. At Ball Gulf, 67% of females produced two egg sacs and 48% produced three sacs. Clutch size declined across the egg sac sequence for all females. Female size, measured as cephalothorax length, was uncorrelated with mean offspring size in all cases. However, larger females produced larger and heavier clutches during 2001 for both populations; female size was uncorrelated with these variables during 2000 at Hardscrabble Creek. Larger clutches from both populations contained more offspring, and larger clutches contained smaller offspring at Hardscrabble Creek in 2001. We found a significant offspring size-number trade-off at Ball Gulf, while at Hardscrabble Creek this trade-off was marginally significant in 2001 and non-significant in 2000.

**Keywords:** Lycosidae, *Pirata*, life history, clutch size, offspring size

The interrelationships among clutch size, offspring size, and female size have been the subject of much empirical and theoretical research, due to the influence of these life history traits on both offspring and parental fitness (see reviews in Clutton-Brock 1991; Roff 1992, 2002; Stearns 1992; Bernardo 1996). Two general results have emerged from this work. The first is the empirical observation that larger females typically produce more and, somewhat less commonly, larger offspring (Roff 1992, 2002; Stearns 1992). The simplest explanation for these relationships is that larger females have more available space in which to store developing offspring (eggs or embryos), although other factors (such as size-based differences in resource usage; see below) may also have an effect.

The second result is the theoretical prediction that clutch size and offspring size should exhibit a trade-off (Smith & Fretwell 1974; Roff 1992, 2002; Stearns 1992). Such a trade-off should exist within individuals because given finite resources for reproduction, females choosing to make larger offspring must necessarily make fewer of them. Empirical evidence for this trade-off has been mixed (see reviews in Roff 1992; Stearns 1992). While many species do exhibit a size-number trade-off, others do not, and the magnitude and direction of the trade-off may vary among populations or among years within a population (e.g., Brown 2001). The lack of a trade-off may be explained by differences among females in their access to resources, such that females of high quality may make both more and larger offspring that low quality females (van Noordwijk & de Jong 1986; Flint et al. 1996; Christians 2000). Thus, female size potentially affects offspring size and number in two ways. Larger females may have more room in which to carry developing offspring, and they may be better able to obtain, defend, store, or allocate (to reproduction) resources.

For spiders, relationships among clutch size, offspring size, and female size have been examined using both inter- and intraspecific data. In comparative studies across species,

[1] Current address: Department of Biology, Box 5063, Tennessee Technological University, Cookeville, TN 38505. E-mail: cabrown@tntech.edu.

female size has been shown to correlate positively with clutch size and/or offspring size (Petersen 1950; Enders 1976; Marshall & Gittleman 1994; Simpson 1995; Prenter et al. 1999), while a size-number trade-off has been found in one study (Simpson 1995) but not another (Marshall & Gittleman 1994). Clutch size also generally increases with female size within a single species (e.g., Briceño 1987; McLay & Hayward 1987; Vollrath 1987; Morse 1988; Tanaka 1992; Simpson 1993; Punzo & Henderson 1999; Buddle 2000), while offspring size may increase with (e.g., Tanaka 1995) or be unrelated to (e.g., Kessler 1971) female size. Intraspecific studies have also found evidence for (Simpson 1993; Tanaka 1995) and against (Simpson 1993) the existence of an offspring size-number trade-off.

Wolf spiders of the genus *Pirata* Sundevall 1833 occur worldwide, predominantly in moist areas such as swamps, bogs, damp forests or meadows and along the shores of ponds or streams. In these habitats they may be one of the most abundant groups of wandering spiders (Nørgaard 1951; Wallace & Exline 1978). Since *Pirata* can easily move on the water as well as on land, they are potentially important conduits of energy and nutrients between aquatic and terrestrial ecosystems. However, their ecology and life histories have received scant attention, particularly among New World species. In this study we report data on clutch size, offspring size, and female size for two populations of the wolf spider *Pirata sedentarius* Montgomery 1904, a widely distributed species found throughout North America and the West Indies (Dondale & Redner 1990). For one population, we also examine changes in clutch size over the breeding season. This represents one of the few studies in which the relationships between these three life history traits have been studied simultaneously within a single species of spider.

## METHODS

We collected *P. sedentarius* females from two locations in western New York. In this area, *P. sedentarius* occurs most commonly in the moist cobble zone along creek banks. The first site was an unnamed creek near the intersection of Creamery Road and Hardscrabble Road, approximately 4.7 km west of West-

field, New York (henceforth the Hardscrabble Creek population). Females were collected here on 21 July 2000 ($n = 17$) and on 22 May ($n = 1$) and 17 July 2001 ($n = 17$). The second site, approximately 33 km ENE of Hardscrabble Creek, was a small tributary of Canadaway Creek running through Ball Gulf in the town of Arkwright, New York (henceforth the Ball Gulf population). Females were collected here from 14–27 June 2001 ($n = 21$). All females were gravid or carrying egg sacs, with the exception of two females from Hardscrabble Creek in 2000 carrying second instar offspring. Gravid females produced an egg sac within seven days of capture, so that effects of captivity (such as changes in food availability) on reproduction should be negligible.

On return to the laboratory, each female was housed individually in a 0.95 L translucent plastic container, fitted with a lid perforated several times to provide air holes. The bottom of the container was lined with a piece of paper toweling which was kept moistened. Females in 2000 also had access to water ad libitum via a one dram shell vial stoppered with a cotton ball. Females were offered 1–2 two-week-old crickets every 5–7 days.

Containers were checked daily for the presence of spiderlings on the female's back or for dispersed spiderlings. For the latter, we considered a clutch to have dispersed if > 50% (by visual inspection) of the offspring were off the female's back. Following dispersal, we weighed each female to the nearest one mg. All live spiderlings in a clutch were weighed together to obtain the total clutch mass (TCM), again to the nearest one mg; we determined mean offspring mass by dividing TCM by clutch size (which included dead spiderlings). After masses were obtained we immediately preserved all spiderlings, living or dead, in 70% ethanol. From each preserved clutch we determined clutch size and, for the 2000 Hardscrabble Creek population only, measured the cephalothorax length (CL, in mm) of 10 randomly selected spiderlings using an Olympus SZ40 dissecting microscope fitted with an optical micrometer. As a measure of investment in reproduction relative to female size, we also calculated relative clutch mass by dividing TCM by female mass.

Because females were being used in an experiment (see below), only seven of the clutches from Hardscrabble Creek in 2001

were allowed to hatch. For the remainder, egg sacs were gently removed from the female using forceps and preserved in 70% ethanol. Clutch size was subsequently determined by counting eggs or larvae.

Females were preserved in 70% ethanol either immediately after offspring dispersal (in 2000) or after being used in a series of trials examining the effect of leg loss on sprint speed (in 2001; P. Apontes & C. Brown, unpub. data). After preservation, female CL was measured (in mm) on a Meiji RZ dissecting microscope equipped with an optical micrometer. Between dispersal of the first clutch and female preservation, many of the Ball Gulf spiders produced a second, and in some cases a third, egg sac. These sacs were removed from the female as produced and preserved in 70% ethanol. Clutch size was then determined by counting eggs. Voucher specimens from each population have been deposited in the American Museum of Natural History, New York.

We examined relationships among the various life history traits using correlation analysis (Pearson's $r$) or least-squares regression on log-transformed data. The trade-off between offspring size and number was examined by first regressing clutch size and offspring size separately against female size, and then using residuals from these regressions in a correlation analysis. This procedure statistically controls for variation in these traits due to female size. Finally, comparisons of life history variables between years or populations were done by ANOVA on log-transformed data, with the exception of relative clutch mass, which was untransformed. All analyses were done using Statistica for Windows version 4.5 (StatSoft 1993).

## RESULTS

A summary of the life history data for the two populations of *P. sedentarius* is presented in Table 1. Most variables exhibited substantial variation, with coefficients of variation (CVs) usually above 20%. The primary exceptions were offspring CL and female CL, which had CVs <10%. Mean offspring mass varied less than did female mass, clutch size, total clutch mass (TCM), or relative clutch mass for both populations. Hardscrabble Creek did not differ between years in female mass ($F_{1, 22}$ = 0.44, $P$ = 0.52), female CL ($F_{1, 31}$

= 2.46, $P$ = 0.13), mean offspring mass ($F_{1, 21}$ = 2.84, $P$ = 0.11), clutch size ($F_{1, 32}$ = 0.001, $P$ = 0.97), TCM ($F_{1, 21}$ = 0.22, $P$ = 0.64), or relative clutch mass ($F_{1, 21}$ = 0.59, $P$ = 0.45). Therefore, data for this population were combined for all subsequent ANOVAs.

Of the 21 Ball Gulf females which produced an initial egg sac, 14 produced a second sac and 10 a third sac. The second egg sac was produced one month (range 31–34 days) after the first sac, and the third sac occurred 2–4 weeks after the second sac (range 14–28 days). For all females clutch size declined in each successive egg sac (Table 1; Fig. 3). However, clutch size was strongly positively correlated across sacs (sac 1 vs. sac 2: $r$ = 0.87, $P$ < 0.001, $n$ = 14; sac 1 vs. sac 3: $r$ = 0.86, $P$ = 0.001, $n$ = 10; sac 2 vs. sac 3: $r$ = 0.81, $P$ = 0.004, $n$ = 10). Comparing first clutches laid in the laboratory indicated that Ball Gulf females produced significantly larger clutches than did Hardscrabble Creek females ($F_{1, 53}$ = 7.11, $P$ = 0.01). However, clutches laid at the same time (Hardscrabble Creek first clutches and Ball Gulf second clutches) were not significantly different in size ($F_{1, 46}$ = 1.02, $P$ = 0.32). Thus, results for Hardscrabble Creek may represent either production of a smaller first clutch or production of a similarly-sized second clutch as compared to Ball Gulf. The latter result seems more likely, given that at least one Hardscrabble Creek female produced an egg sac by late May.

Females from Hardscrabble Creek were larger than their counterparts from Ball Gulf, although this result is only marginally significant for both mass ($F_{1, 40}$ = 3.63, $P$ = 0.06) and CL ($F_{1, 52}$ = 3.77, $P$ = 0.06). However, mean offspring mass did not differ between populations ($F_{1, 39}$ = 0.46, $P$ = 0.50). Total clutch mass ($F_{1, 39}$ = 4.73, $P$ = 0.04) and relative clutch mass ($F_{1, 39}$ = 11.5, $P$ = 0.002) were both significantly higher at Ball Gulf, reflecting the greater clutch sizes in this population.

Female mass and CL were significantly positively correlated in both populations (2000 Hardscrabble Creek: $r$ = 0.80, $P$ < 0.001, $n$ = 16; 2001 Hardscrabble Creek: $r$ = 0.97, $P$ = 0.002, $n$ = 6; 2001 Ball Gulf: $r$ = 0.79, $P$ < 0.001, $n$ = 18). Therefore, we used female CL as our measure of size in the following analyses; using mass gives qualitatively similar results. Since offspring were weighed in both years, we used mass as our
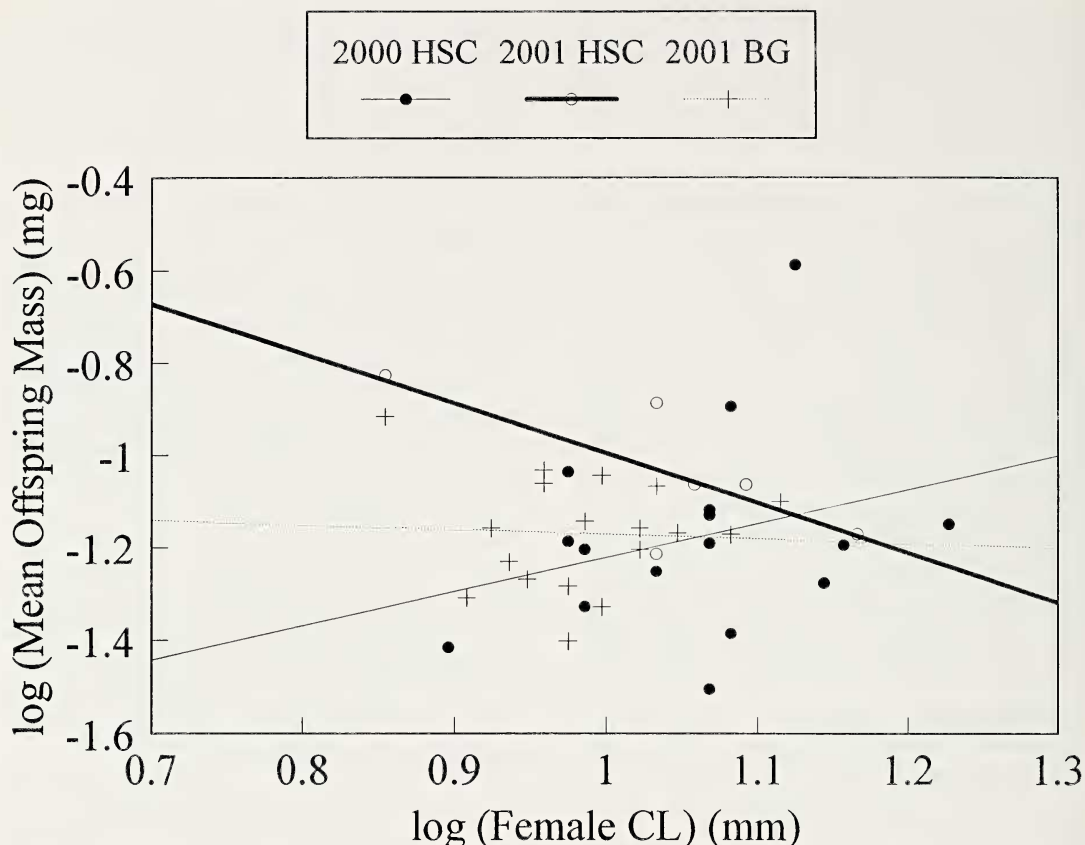
Figure 1.—Linear regressions of mean offspring mass (MOM) against female carapace length (FCL; both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Regression equations: 2000 Hardscrabble Creek: MOM = $-1.96 + 0.74*FCL$, $F_{1,14} = 1.20$, $P = 0.29$, $R^2 = 0.08$; 2001 Hardscrabble Creek: MOM = $0.09 - 1.08*FCL$, $F_{1,4} = 4.52$, $P = 0.10$, $R^2 = 0.53$; Ball Gulf: MOM = $-1.08 - 0.09*FCL$, $F_{1,16} = 0.04$, $P = 0.85$, $R^2 = 0.002$.

measure of offspring size. Using offspring CL gave qualitatively similar results for the 2000 Hardscrabble Creek population, as mass and CL were significantly positively correlated ($r = 0.61$, $P = 0.012$, $n = 16$). Female size was uncorrelated with mean offspring size in both populations and years (Fig. 1). Female size was also uncorrelated with clutch size during 2000 at Hardscrabble Creek (Fig. 2). However, larger females produced larger clutches at Hardscrabble Creek in 2001, and larger first, second, and third clutches at Ball Gulf (Figs. 2, 3). Larger females produced heavier clutches in both populations during 2001, while female size was unrelated to TCM in 2000 (Fig. 4).

Heavier litters contained more offspring in all populations and years (Fig. 5). The relationship between TCM and offspring size was

more complex (Fig. 6). These two variables were uncorrelated for the Ball Gulf and 2000 Hardscrabble Creek populations, while in 2001 at Hardscrabble Creek heavier litters contained smaller offspring. We found a negative relationship between offspring size and number in all population-year combinations (Fig. 7). This trade-off was not significant at Hardscrabble Creek in 2001 ($r = -0.46$, $P = 0.36$, $n = 6$), perhaps due to the low sample size. However, there was a significant size-number trade-off at Ball Gulf ($r = -0.65$, $P = 0.003$, $n = 18$) and a marginally significant trade-off at Hardscrabble Creek in 2000 ($r = -0.50$, $P = 0.06$, $n = 16$).

## DISCUSSION

Our results indicate that *P. sedentarius* females in western New York are capable of
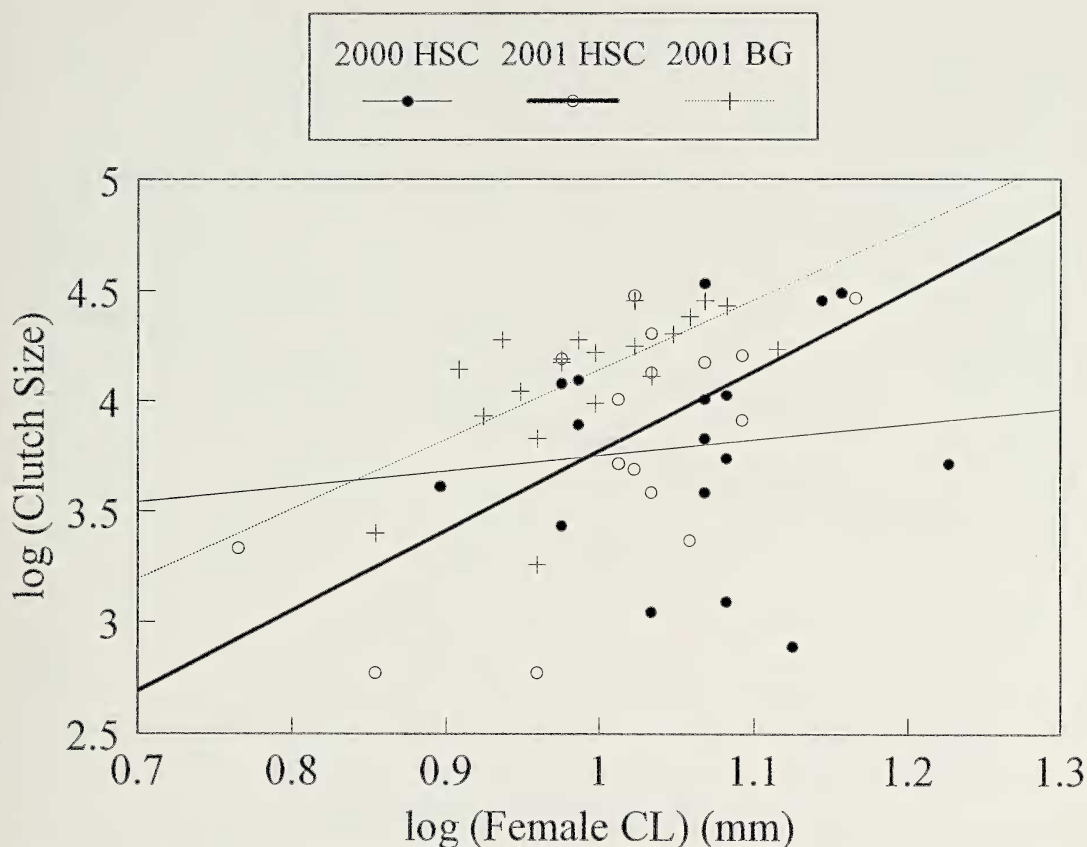
Figure 2.—Linear regressions of initial clutch size (CS) against female carapace length (FCL; both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Regression equations: 2000 Hardscrabble Creek: $CS = 3.05 + 0.70*FCL$, $F_{1,15} = 0.20$, $P = 0.66$, $R^2 = 0.01$; 2001 Hardscrabble Creek: $CS = 0.16 + 3.61*FCL$, $F_{1,14} = 9.29$, $P = 0.009$, $R^2 = 0.36$; Ball Gulf: $CS = 0.98 + 3.16*FCL$, $F_{1,19} = 12.9$, $P = 0.002$, $R^2 = 0.41$.

Table 1.—Summary life history data [mean ± SD (coefficient of variation)] for *Pirata sedentarius*. An unmeasured variable is indicated by NA. CL = cephalothorax length. *Number of litters and females weighed/total number of litters and females measured.

| | Hardscrabble Creek | | Ball Gulf |
| --- | --- | --- | --- |
| | 2000 | 2001 | 2001 |
| Female mass (mg) | 24.1 ± 7.7 (31.8) | 29.3 ± 7.2 (24.7) | 21.8 ± 4.9 (22.4) |
| Female CL (mm) | 2.90 ± 0.23 (8.0) | 2.76 ± 0.30 (9.6) | 2.71 ± 0.17 (6.2) |
| Offspring Mass (mg) | 0.32 ± 0.08 (24.8) | 0.36 ± 0.05 (14.4) | 0.31 ± 0.04 (12.3) |
| Offspring CL (mm) | 0.8 ± 0.05 (6.9) | NA | NA |
| Clutch Size 1 | 49.5 ± 22.9 (46.4) | 50.2 ± 22.6 (45.1) | 64.2 ± 16.1 (25.1) |
| Clutch Size 2 | NA | NA | 40.5 ± 12.5 (30.8) |
| Clutch Size 3 | NA | NA | 24.8 ± 7.6 (30.5) |
| Total Clutch Mass (mg) | 15.1 ± 6.9 (46.1) | 16.7 ± 7.4 (44.5) | 19.0 ± 4.6 (24.2) |
| Relative Clutch Mass | 0.66 ± 0.30 (45.1) | 0.57 ± 0.21 (37.4) | 0.88 ± 0.15 (17.1) |
| Sample Size | 17 | 7/17* | 21 |
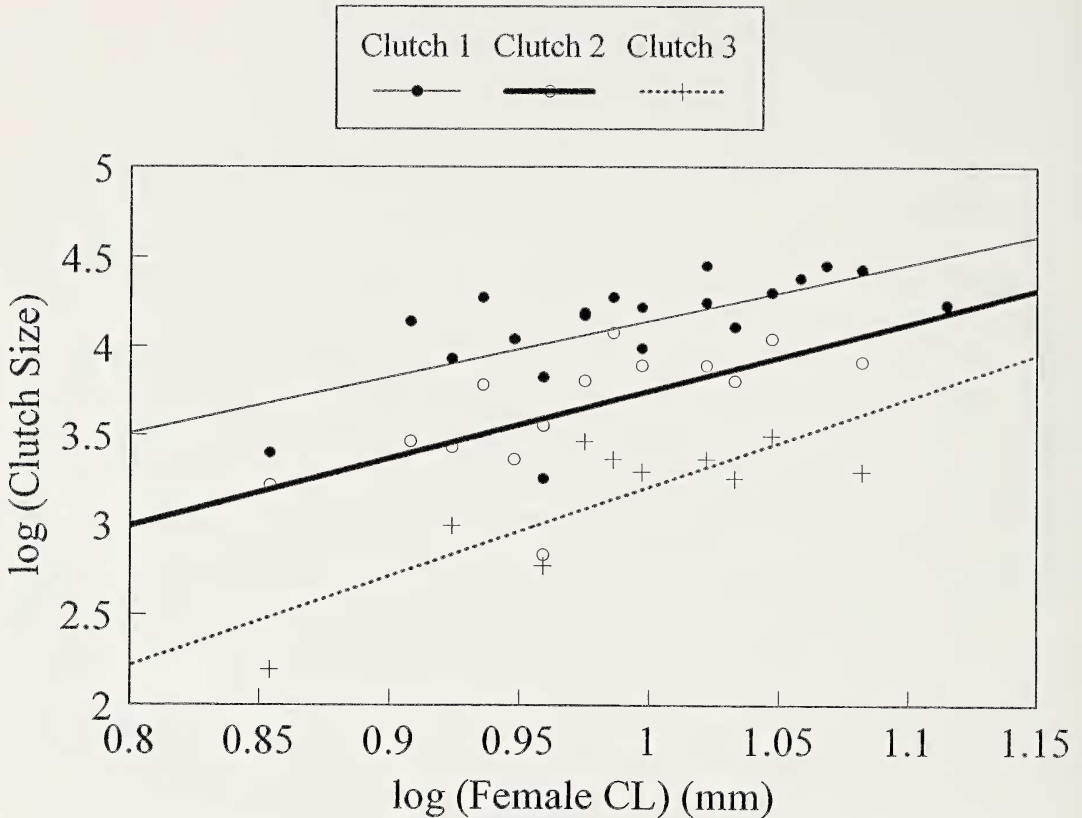
Figure 3.—Linear regressions of clutch size (CS) against female carapace length (FCL; both log transformed) for the first through third egg sacs produced by *Pirata sedentarius* females at Ball Gulf. Regression equations: first clutch: CS = 0.98 + 3.16*FCL, $F_{1,19}$ = 12.9, $P$ = 0.002, $R^2$ = 0.41; second clutch: CS = −0.04 + 3.79*FCL, $F_{1,12}$ = 8.71, $P$ = 0.01, $R^2$ = 0.42; third clutch: CS = −1.75 + 4.96*FCL, $F_{1,8}$ = 15.32, $P$ = 0.004, $R^2$ = 0.66.

producing multiple egg sacs over the course of the breeding season. Whitcomb (1967, cited in Marshall & Gittleman 1994) has also shown that *P. sedentarius* can produce multiple egg sacs, on average 2.5/yr (compared to 2.1 in the present study). We have observed egg sacs in the field as early as mid May and as late as early September in our study populations as well as other populations in western New York. Based on this, we expect that most or all of the initial Ball Gulf sacs produced in the laboratory represent first clutches, while the Hardscrabble Creek sacs are either all second clutches or a mixture of first and second clutches.

While the interclutch interval between sacs one and two (one month) may reasonably approximate natural events, it seems likely to us that the interval between sacs two and three (a minimum of two weeks) was shortened in

at least some spiders. For first sacs produced in the laboratory, the time until hatching ranged from 17–23 days, and offspring were carried for an additional 2–5 days. Thus, unless offspring develop substantially faster in second than in first clutches, our removal of the egg sac led some females to speed up production of the next clutch. Females that lose an egg sac early enough in the breeding season may still then have the ability to produce three (or more) clutches, albeit at the cost of a reduction in overall fecundity.

Mean clutch size for both populations falls within the range (19–93.7) given by Kaston (1946) for five species of *Pirata*. Ball Gulf first clutches are similar in size to the mean values of 63.8 and 54.0 reported for *P. sedentarius* by, respectively, Kaston (1946, under the name *P. maculatus*) and Whitcomb (1967, cited in Marshall & Gittleman 1994). As has
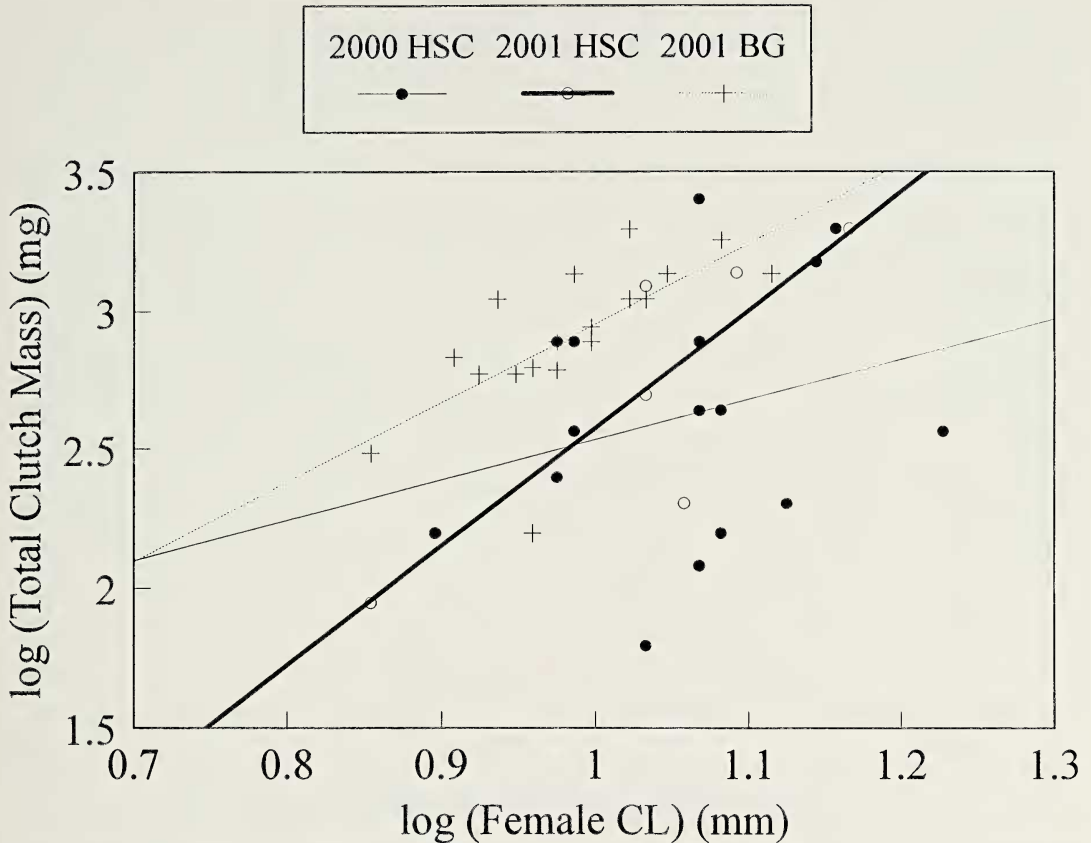
Figure 4.—Linear regressions of total clutch mass (TCM) against female carapace length (FCL; both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Regression equations: 2000 Hardscrabble Creek: TCM = 1.08 + 1.45*FCL, $F_{1,14} = 1.06$, $P = 0.32$, $R^2 = 0.07$; 2001 Hardscrabble Creek: TCM = −1.69 + 4.27*FCL, $F_{1,4} = 8.88$, $P = 0.04$, $R^2 = 0.69$; Ball Gulf: TCM = 0.08 + 2.88*FCL, $F_{1,16} = 13.2$, $P = 0.002$, $R^2 = 0.45$.

been found in a number of other temperate-zone animals (e.g., lizards: Ferguson & Bohlen 1978; birds: Lack 1968; spiders: Foelix 1996), offspring/egg numbers decline over the course of the breeding season (but see Eberhard 1979 for a counterexample in tropical spiders). This decline may be due to a decrease in the amount of resources available to the female for making eggs, or may represent an adaptive shift to the production of fewer, larger offspring which have an increased survival rate when born later in the year (Nussbaum 1981; Ferguson et al. 1982; Roff 1992). Our result showing that Hardscrabble Creek offspring (presumably second clutches) were similar in size to Ball Gulf offspring (first clutches) makes the latter explanation seem less likely for *P. sedentarius*, although this assumes that Hardscrabble Creek first clutches

will also have offspring of similar size. We currently lack sufficient data to address this assumption.

Literature reports of offspring size in *Pirata* are uncommon, but newly emerged spiderlings (as well as adults) of *P. sedentarius* are larger than the corresponding life stage of *P. piraticus* (Clerck 1758) (Yu et al. 2001). Relative clutch mass in *P. sedentarius* was higher than the mean value of 0.5 calculated for 14 species from Table 2 of Marshall & Gittleman (1994), although lower than in several other wandering spiders [e.g., the oxyopid *Peucetia viridans* (Hentz 1832) (Killebrew & Ford 1985); the lycosid *Pardosa lugubris* (Walckenaer 1802) (Edgar 1971)].

During 2001, larger females from both populations produced larger (first, second, and third) clutches, the typical pattern found in
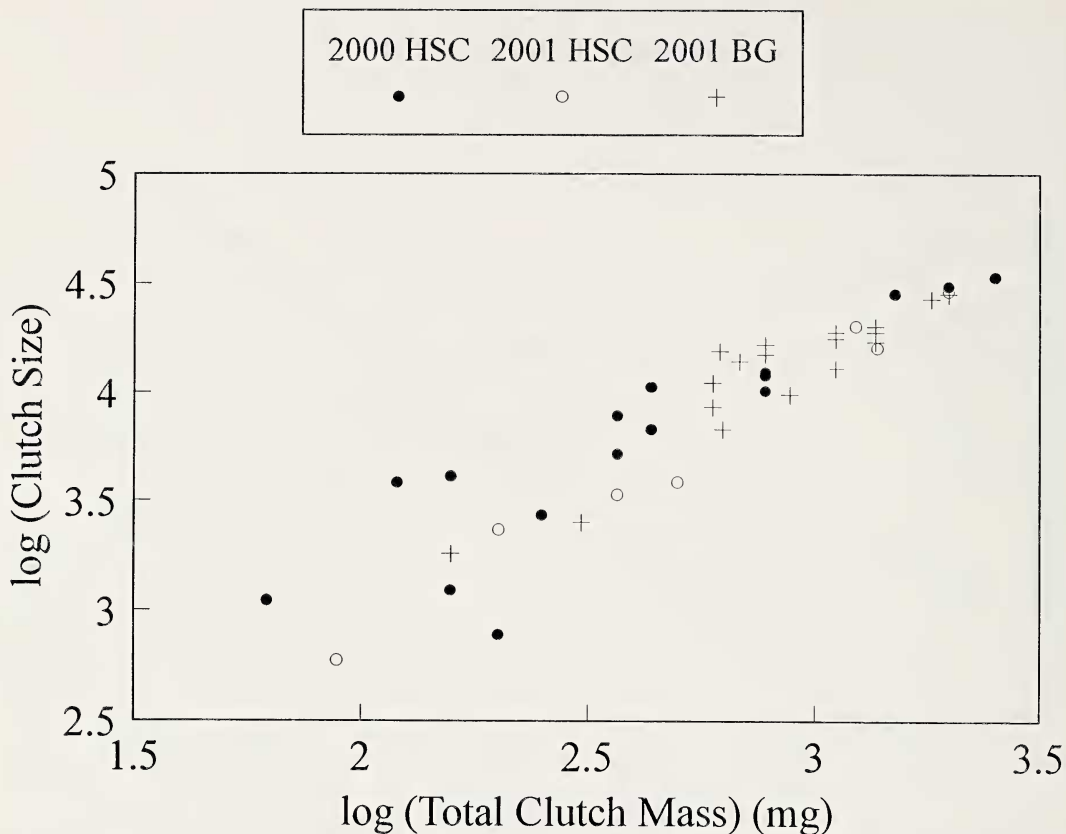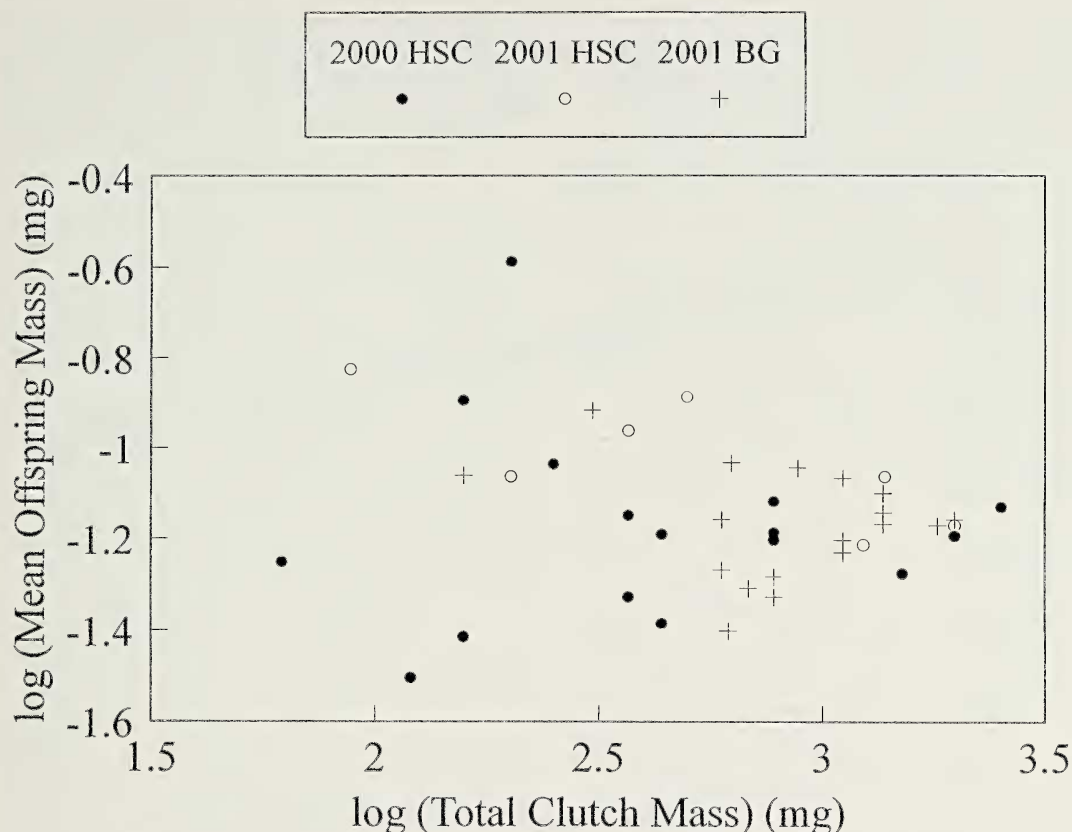
Figure 5.—Correlations between total clutch mass and clutch size (both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Correlations: 2000 Hardscrabble Creek: $r = 0.90$, $P < 0.001$, $n = 16$; 2001 Hardscrabble Creek: $r = 0.99$, $P < 0.001$, $n = 7$; Ball Gulf: $r = 0.93$, $P < 0.001$, $n = 18$.

most invertebrates (reviews in Roff 1992; Stearns 1992), including lycosid (e.g., Petersen 1950; Kessler 1971) and non-lycosid (e.g., Harrington 1978; Austin 1984; Fritz & Morse 1985; Killebrew & Ford 1985; McLay & Hayward 1987; Suter 1990; Punzo & Henderson 1999) spiders. In fact, female size accounted for 36–66% of the variation observed in offspring number during 2001. Larger females also produced heavier clutches in both populations during 2001. The lack of a significant effect of female size on clutch size or mass at Hardscrabble Creek in 2000 was therefore surprising, particularly given that neither female size, clutch size nor TCM varied between years in this population. An examination of the regression equations (Fig. 2) shows that relatively small females produced larger, heavier clutches in 2000 than in 2001, while relatively large females produced larger, heavier clutches in 2001. This suggests that

resources available to females differed among years, and only smaller females were in good enough condition (i.e., obtained enough resources) during 2000 to produce a normal clutch for their size. Differences in residual condition indices (residuals from the regression of female mass on CL; Jakob et al. 1996) were in the predicted direction (2001: mean ± SD = 0.26 ± 0.24; 2000: mean ± SD = −0.09 ± 1.12), although the lack of significance ($F_{1, 21} = 0.57$, $P = 0.46$) indicates at best weak support for this hypothesis.

Contrary to the results for clutch size, female size was unrelated to offspring size in either population. This appears to be a common result in spiders (e.g., Kessler 1971; McLay & Hayward 1987; Killebrew & Ford 1985) and other arachnids (Brown 2001), although a number of other invertebrate taxa do exhibit an increase in offspring size with female size (reviewed in Roff 1992). Recalling

Figure 6.—Correlations between total clutch mass and mean offspring mass (both log transformed) for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*. Correlations: 2000 Hardscrabble Creek: $r = -0.20$, $P = 0.46$, $n = 16$; 2001 Hardscrabble Creek: $r = -0.76$, $P = 0.046$, $n = 7$; Ball Gulf: $r = -0.20$, $P = 0.42$, $n = 18$.

that offspring size varies less among females than other traits, our results indicate that offspring size in *P. sedentarius* is relatively canalized compared to offspring number. This may represent an anatomical constraint, perhaps in the structure of the ovaries or epigynum, which limits egg size but is itself unrelated to female size. Alternatively, females may exhibit little variation in per-offspring allocation strategies. For example, females may provision eggs with some minimum amount of yolk necessary for survival until offspring dispersal (see Marshall & Gittleman 1994), in which case females can maximize clutch size dependent on their available energy stores. This latter scenario potentially establishes a conflict of interest between the female and her offspring (sensu Parker & Mock 1987; Godfray & Parker 1991), as larger offspring size increases early-life fitness (starvation resis-

tance) in at least one species of spider (Tanaka 1995).

As predicted by much life history theory (Roff 1992, 2002; Stearns 1992), offspring size and number appear to trade off in *P. sedentarius*. However, as has been found in other arachnids (e.g., Simpson 1993; Brown 2001), the strength of this trade-off within a species may vary among populations or over time. For example, our results at Hardscrabble Creek echo those of Simpson (1993) on the arctic lycosid *Pardosa glacialis* (Thorell 1872). He found that *P. glacialis* exhibited a trade-off in one year of his study but not another [and he found no trade-off in a second species, *Alopecosa hirtipes* (Kulczynski 1908), during either year]. There exist relatively few intraspecific studies of the size-number trade-off in spiders, with some documenting a size-number trade-off (e.g.,
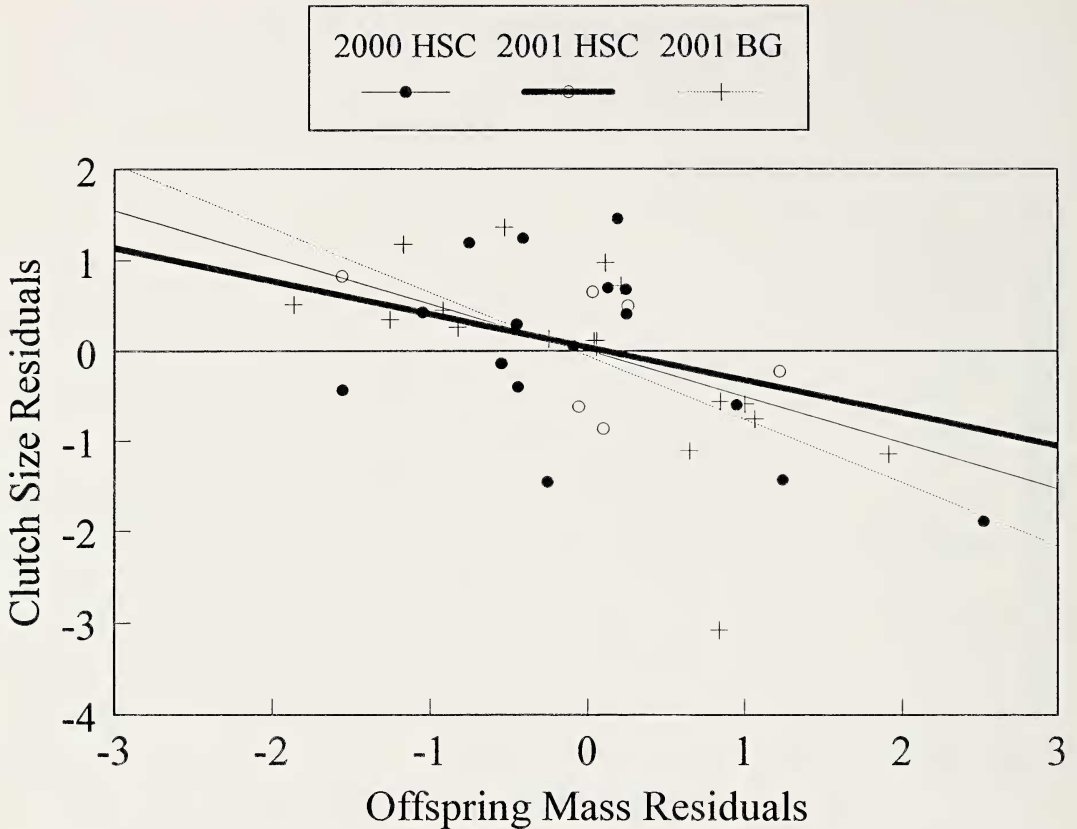
Figure 7.—Correlations between residual clutch size and residual offspring mass for the Hardscrabble Creek and Ball Gulf populations of *Pirata sedentarius*.

Simpson 1993; Tanaka 1995) and others not (e.g., Fritz & Morse 1985; Simpson 1993).

The difficulty with consistently detecting a size-number trade-off in spiders may reflect the strong food limitation in many species (Wise 1993), such that many individuals will not obtain sufficient resources to produce a "normal" size or number of offspring. This may lead to a positive relationship between offspring size and number, if higher quality females (those obtaining the most resources) produce both more and larger offspring. It might also lead the trade-off slope to flatten out, if some (e.g., smaller) females are able to allocate a higher percentage of their resources to reproduction than other (e.g., larger) females because of differences in maintenance energy requirements. This situation could arise even if the latter (larger) females obtained equal or greater total amounts of resources. The relative canalization of offspring size might also help explain the lack of a size-

number trade-off. If females all produce offspring of similar size, either because of an inability or unwillingness to deviate substantially from a species-specific egg size, then the underlying decision process for the trade-off (adding excess energy either to offspring already made or to the production of new offspring) is rendered moot. Instead, females will simply make as many offspring of a given, perhaps minimally viable, size as their resources allow. Regardless of mechanism, determining why, how, and under what circumstances trade-offs occur remains a critical challenge for the understanding of arachnid life history evolution.

## ACKNOWLEDGMENTS

Buckle, Theo Blick, Volker Framenau, and especially Peter Smithers and David Mayntz for the citations from BAZAR. We also thank two anonymous referees for their critical comments on the first draft.

## LITERATURE CITED

Austin, A.D. 1984. Life history of *Clubiona robusta* L. Koch and related species (Araneae, Clubionidae) in South Australia. Journal of Arachnology 12:87–104.

Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. American Zoologist 36:216–236.

Briceño, R. 1987. How spiders determine clutch size. Revista de Biologia Tropical 35:25–29.

Brown, C.A. 2001. Allometry of offspring size and number in scorpions. Pp. 307–315. *In* Scorpions 2001. In Memoriam Gary A. Polis. (V. Fet & P. A. Selden, eds.). British Arachnological Society, Burnham Beeches, United Kingdom.

Buddle, C.M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28:319–328.

Christians, J.K. 2000. Trade-offs between egg size and number in waterfowl: an interspecific test of the van Noordwijk and de Jong model. Functional Ecology 14:497–501.

Clutton-Brock, T.H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton, New Jersey.

Dondale, C.D. & J.H. Redner. 1990. The Insects and Arachnids of Canada. Part 17. The Wolf Spiders, Nurseryweb Spiders, and Lynx Spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Canadian Department of Agriculture Publications, Ottawa.

Eberhard, W. 1979. Rates of egg production by tropical spiders in the field. Biotropica 11:292–300.

Edgar, W.D. 1971. Seasonal weight changes, age structure, natality and mortality in the wolf spider *Pardosa lugubris* Walck. in central Scotland. Oikos 22:84–92.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69:991–998.

Ferguson, G.W. & C.H. Bohlen. 1978. Demographic analysis: a tool for the study of natural selection of behavioral traits. Pp. 227–243. *In* Conference on Behavior and Neurology of lizards. (N. Greenberg & P. MacLean, eds.). DHEW Publication No.(ADM) 77–491, Washington, DC.

Ferguson, G.W., K.L. Brown & V.G. DeMarco. 1982. Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. Herpetologica 38:178–188.

Flint, P.L., J.B. Grand & J.S. Sedinger. 1996. Allocation of limited reserves to a clutch: a model explaining the lack of a relationship between clutch size and egg size. Auk 113:939–942.

Foelix, R.F. 1996. Biology of Spiders. Second Edition. Oxford University Press, Oxford.

Fritz, R.S. & D.H. Morse. 1985. Reproductive success and foraging of the crab spider *Misumena vatia*. Oecologia 65:194–200.

Godfray, H.C.J. & G.A. Parker. 1991. Clutch size, fecundity and parent-offspring conflict. Philosophical Transactions of the Royal Society of London B 332:67–79.

Harrington, C.L. 1978. Field studies on reproduction in the funnel-web spider *Agelenopsis potteri* (Araneae; Agelenidae). Oikos 31:368–375.

Jakob, E.M., S.D. Marshall & G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Kaston, B.J. 1946. Spiders of Connecticut. Connecticut State Geological and Natural History Survey, Bulletin No. 70.

Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8:93–109.

Killebrew, D.W. & N.B. Ford. 1985. Reproductive tactics and female body size in the green lynx spider, *Peucetia viridans* (Araneae, Oxyopidae). Journal of Arachnology 13:375–382.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8:118–124.

McLay, C.L. & T.L. Hayward. 1987. Reproductive biology of the intertidal spider *Desis marina* (Araneae: Desidae) on a New Zealand rocky shore. Journal of Zoology 211:357–372.

Morse, D. 1988. Relationship between crab spider *Misumena vatia* nesting success and earlier patch-choice decisions. Ecology 69:1970–1973.

Nørgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. Oikos 3:1–21.

Nussbaum, R.A. 1981. Seasonal shifts in clutch-size and egg-size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. Oecologia 49:8–13.

Parker, G.A. & D.W. Mock. 1987. Parent-offspring conflict over clutch size. Evolutionary Ecology 1:161–174.

Petersen, B. 1950. The relation between size of mother and number of eggs and young in some spiders and its significance for the evolution of size. Experientia 6:96–98.

Prenter, J., R.W. Elwood & W.I. Montgomery. 1999. Sexual size dimorphism and reproductive

investment by female spiders: a comparative analysis. Evolution 53:1987–1994.

Punzo, F. & L. Henderson. 1999. Aspects of the natural history and behavioral ecology of the tarantula spider, *Aphonopelma hentzi* (Orthognatha, Theraphosidae). Bulletin of the British Arachnological Society 11:121–128.

Roff, D.A. 1992. The Evolution of Life Histories. Chapman & Hall, New York.

Roff, D.A. 2002. Life History Evolution. Sinauer Associates, Sunderland, Massachusetts.

Simpson, M.R. 1993. Reproduction of two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. Canadian Journal of Zoology 71:451–457.

Simpson, M.R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76:795–800.

Smith, C.C. & S.D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

StatSoft. 1993. Statistica for Windows, version 4.5. StatSoft, Tulsa, Oklahoma.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Suter, R.B. 1990. Determinants of fecundity in *Frontinella pyramitela* (Araneae, Linyphiidae). Journal of Arachnology 18:263–269.

Tanaka, K. 1992. Life history of the funnel-web spider *Agelena limbata*: web site, growth, and reproduction. Acta Arachnologica 41:91–101.

Tanaka, K. 1995. Variation in offspring size within a population of the web-building spider *Agelena limbata*. Researches in Population Ecology 37:197–202.

van Noordwijk, A.J. & G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Vollrath, F. 1987. Growth, foraging, and reproductive success. Pp. 357–370. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Wallace, H.K. & H. Exline. 1978. Spiders of the genus *Pirata* in North America, Central America and the West Indies (Araneae, Lycosidae). Journal of Arachnology 5:1–112.

Whitcomb, W. 1967. Wolf and lynx spider life histories. Terminal report to the National Science Foundation, Washington, DC.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK.

Yu, P., J. Zhao & H. Cui. 2001. The morphological characters and growth of spiderlings of *Pirata piraticus* (Clerck). Acta Arachnologica Sinica 10:22–25.